



ORIGINAL
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A modern pollen rain study from the central Andes region of South America

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ABSTRACT

Aim To provide a greater understanding of the modern pollen rain for the central Andes region of South America, thus laying the groundwork for future pollen studies and the derivation of pollen-climate transfer functions and response surfaces.

Location Peru, Bolivia and Chile.

Methods Standard palynological techniques for surface soil sampling and discriminant analysis.

Results Statistical analysis of the 40 surface samples revealed four palynologically distinct assemblages: (1) the Yungas on the eastern slopes of the Andes; (2) the puna grasslands of the Altiplano; (3) the Coastal Deserts to the west of the Andes; and (4) the Southern Bolivian Highlands.

Main conclusions The Yungas group is characterized by high percentages of Urticaceae/Moraceae pollen and fern spores along with trace amounts of pollen from common zoophilous lowland taxa such as Piperaceae, Bignoniaceae and Malpighiaceae. The puna assemblage of the Altiplano is characterized by the dominance of grass (Poaceae) in combination with moderate frequencies of Asteraceae pollen, which tend to increase slightly towards the southern (drier) locations of the Altiplano. Lower percentages of grass pollen and the greater prevalence of Asteraceae, Solanaceae, and the Chenopodiaceae/Amaranthaceae families define the coastal deserts to the west of the Andes. Samples taken from the Southern Bolivian Highlands are characterized by the dominance of Solanaceae in the area, in combination with the pollen of other xerophytic taxa.

Keywords

Altiplano, Andes, biogeography, Bolivia, Chile, modern pollen rain, palynology, Peru.

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INTRODUCTION

In order for palynologists to reconstruct past environments accurately with fossil pollen evidence, it is necessary to first understand how the current vegetation is represented in the modern pollen rain of the study area (Webb *et al.*, 1987, 1993). In the central Andes region of South America, however, no comprehensive study of this nature exists to date. Of the dozen or so fossil pollen studies that have been conducted (e.g. Graf, 1981; Hansen *et al.*, 1984, 1994, 2003; Markgraf, 1985; Baied & Wheeler, 1993; Hansen & Rodbell, 1995; Holmgren *et al.*, 2001; Latorre *et al.*, 2002, 2003; Paduano *et al.*, 2003), only a few have incorporated a modern pollen rain study into their work

(i.e. Graf, 1981; Hansen *et al.*, 1984, 2003; Hansen & Rodbell, 1995). These studies are highly localized though, and only represent the areas immediately surrounding their respective study sites. Comprehensive modern pollen studies do exist in other areas of South America, such as Brazil and Ecuador (Bush *et al.*, 2001), southern Peru (Weng *et al.*, 2004), Colombia (Grabandt, 1980) and southern Chile (Haberle & Bennett, 2001; Markgraf *et al.*, 2002). However, except for a short elevational transect in southern Peru along 12° S (Weng *et al.*, 2004), these studies are too far removed from the Andean Altiplano to offer any assistance in establishing a modern analogue.

This research is a systematic analysis of the modern pollen rain in the central Andes region of South America between 13°

and 22° S. The results are derived from 40 surface soil samples collected from the countries of Peru, Bolivia, and Chile during June and July of 2001. These data will help to broaden our understanding of the modern relationships among pollen and vegetation in the region, and fill a large gap in the pollen data network from South America.

STUDY AREA

The study area, encompassing the 40 surface soil samples, lies roughly between 13° and 22° S latitude and between longitudes 66° and 72° W (Fig. 1). At the centre of the study area is the Andean Altiplano. This plateau is the second highest in the world and covers approximately 100,000 km² across Peru, Bolivia and Chile. It is a dry and windswept environment that straddles the rainshadow of the Andes Mountains, and averages 4000 m in elevation (Hastenrath, 1985). In general, this region has a strong north-east to south-west precipitation gradient, with precipitation totals diminishing towards the Atacama Desert in northern Chile (Latorre *et al.*, 2002). Annual precipitation totals in the eastern sections of the Altiplano usually average well over 700 mm, while the westernmost sections typically produce 200–400 mm (Garreaud *et al.*, 2003). Precipitation is highly seasonal on the Altiplano with over 80% of the annual precipitation falling between December and March (Vuille *et al.*, 1998). This wet season corresponds with the moisture-laden easterly winds that dominate the Altiplano during the austral summer between November and March as a result of the circulation pattern produced by the South American Summer Monsoon (Zhou & Lau, 1998). The prevailing winds for the remainder of

the year are decidedly north-westerly (Virji, 1981; Hardy *et al.*, 1998; Vuille *et al.*, 1998; Garreaud *et al.*, 2003).

To either side of the plateau are steep environmental gradients, which become increasingly wetter on the eastern slopes and increasingly drier towards the west (Vuille *et al.*, 1998). Although the majority of the Altiplano is a relatively flat region, some areas have an extremely complex topography. Numerous mountain ranges litter the landscape, some of which support peaks that often reach 6000 m in height. Towards the southern extent of the Altiplano is an area referred to by the authors as the Southern Bolivian Highlands. This scrub desert environment (Arroyo *et al.*, 1988) is unique from the rest of the Altiplano, and is dotted with salt lakes (salar) and sedimentary rock formations, some of which date back to the Cretaceous Period (Holmgren *et al.*, 2001).

The 40 surface samples (Table 1) were collected along three different transects (Fig. 2). Two of the transects run from the Pacific coasts of Peru and Chile, through the Sechura and Atacama deserts, respectively, and up the western slopes of the Andes. From here they both continue across the Altiplano and descend the eastern slopes of the Andes, finally terminating in the lower reaches of the Yungas. The third transect begins just north of Cusco, Peru and winds south-eastward through the Altiplano, terminating at San Vicente, Bolivia in the heart of the Southern Bolivian Highlands. These transects were chosen because they encompass every major vegetation zone in the central Andes. These surface samples will provide the first modern pollen rain data for some of these important vegetation communities.

Vegetation and climate

The vegetation of the Altiplano is most often categorized as puna, named after the 'puna-brava' vegetation community that dominates the landscape (Tosi, 1960). Puna and its variants, commonly occurring between 5000 and 3300 m, are essentially dry grasslands dominated by bunch grasses like *Festuca* and *Stipa* (Poaceae) (Hansen *et al.*, 1984). In depressions or low-lying areas near sources of water, the marsh-like 'bofedales' community can occur (Baied & Wheeler, 1993). Bofedales is a cushion-peat bog habitat that supports a wide range of hydrophilous plants, including the tussock grasses (Poaceae), yareta (*Azorella yarita*, a cushion plant of the family Apiaceae), Cyperaceae, Juncaceae, and aquatic plants like *Isoetes* and *Myriophyllum* (Haloragidaceae).

Although the puna ecosystem is relatively homogeneous throughout its range, it is commonly divided into three subregions, which are largely a function of elevation. The upper reaches of the puna, known as superpuna, occur between c. 5000 (snowline) and 4300 m (Hansen *et al.*, 1984). Superpuna as a region averages approximately 4 °C annually with freezing temperatures occurring almost daily (Tosi, 1960). Annual precipitation totals range from 100 to 200 mm in the arid southern sections (Latorre *et al.*, 2002; Garreaud *et al.*, 2003) to over 500 mm in more northern locations (Hansen *et al.*, 1984). However, 50–85% of this is lost to runoff

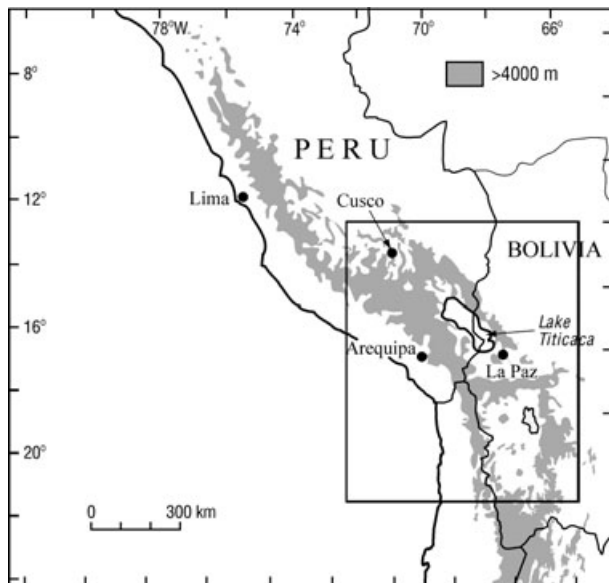


Figure 1 Map of the Central Andes, South America (adapted from Reese *et al.*, 2003). The inset box shows the approximate study area.

Table 1 Location data for the 40 Andean surface samples. The material collected for each sample was topsoil except for samples 32–36, which were sand

Sample no.	Group no.	Latitude (°S)	Longitude (°W)	Altitude (m)	Vegetation type
1	1	13.369	71.604	3450	Yungas
2	1	13.275	71.596	2976	Yungas
3	1	13.205	71.617	3329	Yungas
4	1	13.156	71.588	2329	Yungas
5	1	13.036	71.524	1271	Yungas
6	1	12.889	71.361	463	Yungas
7	1	15.128	67.042	230	Yungas
8	1	15.517	67.245	611	Yungas
9	1	15.983	67.517	3499	Yungas
10	1	16.088	67.697	3502	Yungas
11	1	16.299	67.819	2987	Yungas
12	2	13.449	71.654	3908	Altiplano
13	2	13.841	71.541	4063	Altiplano
14	2	13.930	70.857	5108	Altiplano
15	2	13.907	70.940	4680	Altiplano
16	2	14.225	71.217	3783	Altiplano
17	2	14.486	71.297	4171	Altiplano
18	2	14.601	70.832	4002	Altiplano
19	2	14.737	71.351	4011	Altiplano
20	2	15.171	70.358	3890	Altiplano
21	2	15.382	71.271	4302	Altiplano
22	2	15.777	70.035	3885	Altiplano
23	2	16.070	71.557	3894	Altiplano
24	2	16.273	69.209	3855	Altiplano
25	2	16.414	68.053	4337	Altiplano
26	2	17.282	67.991	3798	Altiplano
27	2	17.460	67.488	3819	Altiplano
28	2	17.750	68.430	3983	Altiplano
29	2	18.107	68.934	4580	Altiplano
30	2	18.196	69.529	3989	Altiplano
31	2	18.560	66.946	3732	Altiplano
32	3	16.425	71.677	1957	Desert
33	3	16.613	71.864	1393	Desert
34	3	16.935	72.060	698	Desert
35	3	18.425	70.042	734	Desert
36	3	18.464	69.804	2190	Desert
37	4	19.557	66.866	3820	Southern Bolivian Highlands
38	4	20.316	66.981	3666	Southern Bolivian Highlands
39	4	20.840	66.357	3933	Southern Bolivian Highlands
40	4	21.503	66.131	4028	Southern Bolivian Highlands

(Hansen *et al.*, 1984). The plants that dominate the superpuna are adapted to this harsh environment and include *Plantago*, *Ephedra*, Caryophyllaceae, Asters like *Gynoxys* and *Baccharis*, *Azorella*, and the bunch grasses. *Polylepis*, the small Rosaceae tree, can also occur up to 5100 m (Kessler, 1995; Braun, 1997), although obviously out of its optimal range.

Standard puna commonly occurs between 4300 and 3900 m (Tosi, 1960; Cuatrecasas, 1968). This subregion is similar to the superpuna, however, the mean annual temperature is slightly warmer at 7 °C, while precipitation increases and ranges from 400 to 800 mm annually (Hansen *et al.*, 1984; Garreaud *et al.*, 2003). Grasses become increasingly abundant in this region, along with greater numbers of trees and shrubs like *Polylepis*, Ericaceae and *Cupressus*. Below the puna proper lies the subpuna (c. 3900–3300 m). Subpuna is primarily

limited to the eastern, or wetter side of the Andean Altiplano, where *Dodonaea*, *Rapanea* and *Alnus* become regular elements of the ecosystem.

The altitudinal zonation of the puna is further complicated by the north-east (wet) to south-west (dry) precipitation gradient of the region, which also impacts the vegetational composition of the puna ecosystem. This gradient is responsible for an 80% reduction in species richness and a 50% loss in ground cover in the southern and western sections, as compared with the north-east (Arroyo *et al.*, 1988). The abundance of grass pollen has proven to be a good indicator of the precipitation gradient across the Altiplano, as the percentage of grass tends to increase with increased precipitation (Meserve & Glanz, 1978; Betancourt *et al.*, 2000; Latorre *et al.*, 2002, 2003).

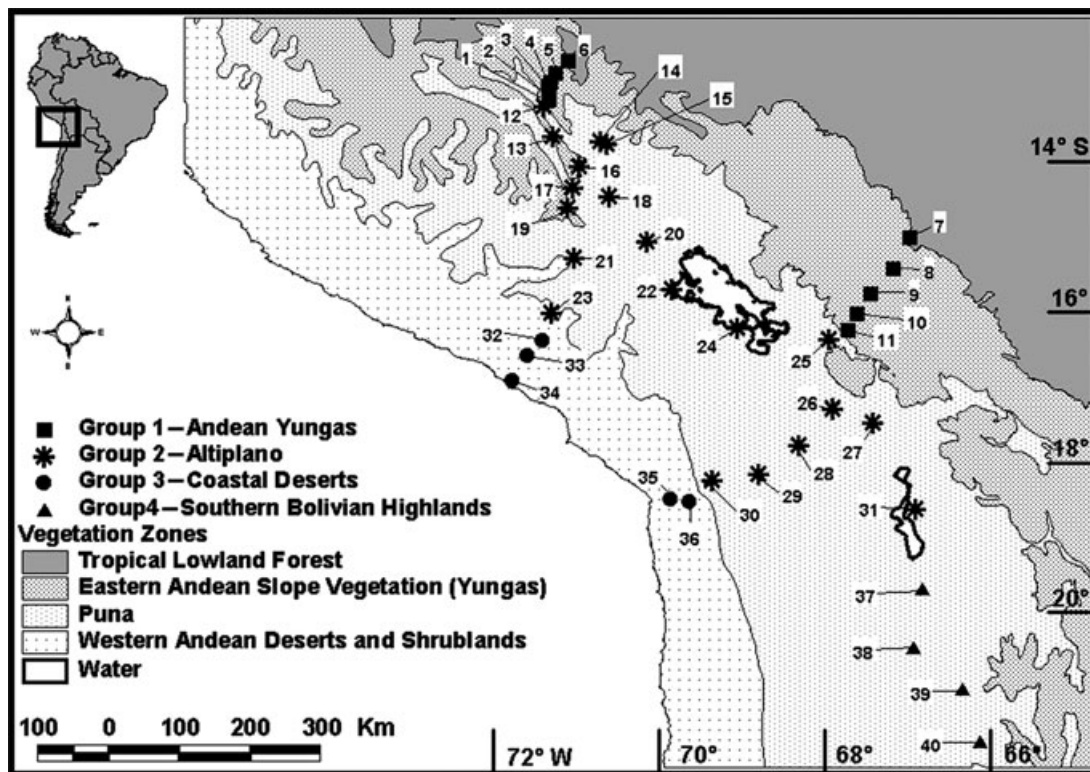


Figure 2 Map of the central Andes showing the location of the 40 surface samples and their respective groups (classifications), in relation to the major vegetation zones of the region (ecoregions defined by Olson *et al.*, 2001).

To the east of the Altiplano, below the subpuna, lies the steep environmental gradient of the Andean slopes that can often change from puna-like vegetation to tropical wet (Af, Köppen) or dry (Aw, Köppen) forest in a horizontal distance of 200 km in some areas (Reese & Liu, 2002). Below 3000 m in the Yungas (Weberbauer, 1936, 1945), nearly all puna species are absent and the vegetation is lush with arboreal ferns (e.g. *Cyathea* spp.), epiphytes, lianas and trees. The notable exceptions are disturbed areas, where elements of the subpuna are allowed to invade (Hansen *et al.*, 1984). Typical tree species include *Alnus*, *Myrica*, *Podocarpus*, *Juglans*, *Weinmannia*, *Rapanea*, *Escallonia*, and members of the Apocynaceae, Ericaceae, Myrtaceae, Melastomataceae, and the Urticaceae and Moraceae families. *Cecropia* is a common tree on disturbed sites. Below this vegetation zone, where human disturbance has not encroached, tropical wet or dry forest occurs. Extensive research has been done on the biodiversity of this ecosystem (i.e. Gentry, 1993), where plant families such as Bignoniaceae (e.g. *Jacaranda*), Melastomataceae (e.g. *Miconia*), Piperaceae (*Piper* spp.), Malpighiaceae (*Malpighia* spp.) and Araceae are common.

From the western slopes of the Andean Altiplano down to the Pacific coast, the vegetation is quite different and much less complex than the eastern slopes. Here, the vegetation is predominantly a shrub desert, although in some areas elements of the puna ecosystems can extend all the way to the Pacific Ocean. Desert taxa, such as Chenopodiaceae (Goosefoot family), Amaranthaceae (Amaranth family), Asteraceae, Cactaceae, Euphorbiaceae, *Plantago* and *Ephedra* are most

common. Although trees such as *Prosopis* are abundant in the wetter sections of the western coast below 1500 m, they hardly ever form dense stands (Reese & Liu, 2002).

The vegetation and landscape change remarkably in the southern part of the Altiplano – a region we refer to as the Southern Bolivian Highlands. Although this region is undifferentiated from the Altiplano on a global-scale map of ecoregions (Olson *et al.*, 2001), the vegetation changes from puna to a scrub desert (Arroyo *et al.*, 1988). Here the grasses (Poaceae) are no longer the dominant vegetation type, as they are replaced by xerophytic shrubs belonging to the Solanaceae (Nightshade), Chenopodiaceae, Amaranthaceae, Asteraceae, and Euphorbiaceae families. Scrubs of the Solanaceae family, especially *Fabiana*, are dominant between 3200 and 4000 m (Latorre *et al.*, 2002). Our field observations as well as our modern pollen rain data (see below) suggest that it is appropriate to distinguish the Southern Bolivian Highlands as a separate vegetation zone from the Altiplano or puna of Peru and northern Bolivia. Although the Southern Bolivian Highlands share many floristic elements with the western Andean slopes, it is distinct from the latter vegetation zone by the prevalence of Solanaceae shrubs, by the abundance of salt lakes and dried lake beds, and by its high elevations.

MATERIALS AND METHODS

In June and July of 2001, 40 surface soil samples were collected with a systematic point sampling scheme along three transects

running through the central Andes region of Peru, Bolivia and Chile (Fig. 2). Samples were only collected from sites that had not been visibly altered by human disturbance. Considering the long history of human occupation in the region, finding these ideal sampling environments proved to be a challenging task, which in part explains the low number of suitable samples that were collected for this study. In all cases, topsoil and/or sand was collected and sealed into Whirlpack plastic bags.

All samples were processed for pollen following the standard procedures (Faegri & Iversen, 1975). For the majority of the surface samples, 0.9 cc of sediment was selected for analysis. However, for the extremely sandy samples, 10.0 cc of material was chosen and subjected to a pollen separation technique using sodium pyrophosphate (Cwynar *et al.*, 1979). After these initial steps, the samples were treated with a series of acids and bases, namely hydrochloric acid (to remove carbonates), potassium hydroxide (to remove organics), hydrofluoric acid (to remove silicates) and acetolysis solution (to remove cellulose). After these treatments, the residue was stained with safranin and mounted onto microscope slides with silicone oil. Pollen grains and fern spores were counted until 300 were identified. Pollen percentages were calculated using TILIA computer software, and were based on a sum of all pollen and spores. TILIA GRAPH for Windows was used to generate all pollen diagrams. Discriminant analysis was performed on the pollen percentage data using SPSS (SPSS, Inc. Chicago, IL, USA) version 11.5.

RESULTS

The 40 surface soil samples (Table 1) were divided into four groups based on their location and corresponding ecoregion (ecoregions defined by Olson *et al.*, 2001) (Fig. 2). Group 1 (samples 1–11) corresponds to the soil samples taken from the eastern Andean slopes (Yungas). Group 2 (samples 12–31) included the samples taken from the puna grasslands of the Andean Altiplano. The samples in this group are numbered and arranged according to latitude, with the most northerly location numbered 12 and the most southerly location numbered 31. This arrangement should reflect the changes in vegetation assemblage that are associated with the north-east to south-west precipitation gradient that exists in the area. Group 3 (samples 32–36) consists of samples taken from the Atacama and Sechura deserts on the west coast of South America. Group 4 (samples 37–40) consisted of the four samples located in the scrub desert of the Southern Bolivian Highlands, where the Solanaceae plant family is dominant. Although the World Wildlife Fund Ecoregions Report (Olson *et al.*, 2001) does not distinguish this region from the puna grasslands of the Altiplano, this group was delineated based on marked differences in both landform and vegetation (which are also reflected in a distinct modern pollen assemblage from that of the puna grasslands, see below).

Although each surface sample was assigned to a major vegetation region based on its geographical location, in practice this is often arbitrary as vegetation boundaries are

transitional and difficult to recognize in the field. Moreover, patterns of vegetation at the local scale are often heterogeneous, with small azonal vegetation communities existing within a broad vegetation region. For example, the marsh-like 'bofedales' community often occurs in small basins near sources of water. This community is dominated by *Azorella* and hydrophilous herbs (e.g. Cyperaceae); a stark contrast to the semi-arid puna grasslands that surround them. Therefore, great care was taken in the field to ensure that each pollen sample was collected from sites representing the dominant vegetation community, and from more open sites that would reflect a more regional instead of local (*sensu* Jacobson & Bradshaw, 1981) pollen signal. The latter objective was more difficult on the densely-vegetated eastern slopes of the Andes. In this mountainous environment the pollen signal may be further complicated by the amount of upslope pollen transport by the prevailing wind (Maher, 1963; Flenley, 1979; Markgraf, 1980; Solomon & Silkworth, 1986; Spear, 1989; Bush, 2000). Above the treeline on the Altiplano, the input of pollen from regional and distant sources is quite common (Hansen *et al.*, 1984; Bush, 2000).

After these four groups were delineated based on field observations and map referencing, discriminant analysis (SPSS) was used to validate these groups. Discriminant analysis is an effective tool to objectively evaluate the prior classification of surface pollen samples into groups (Liu & Lam, 1985; Lynch, 1996). The stepwise method of discriminant analysis was used for this study (Klecka, 1980). This method analyses each variable (pollen taxon), one at a time, for entry into the discriminant function by utilizing a process of forward selection (if a variable's *F* probability is > 0.05) and backward elimination (if a variable's *F* probability < 0.10). If a variable is selected into the equation (discriminant function), it is then re-evaluated after each iteration for possible elimination. Variables are entered into and then removed from the equation until no more meet the removal criteria. The remaining variables are then used in the discriminant function. Nine pollen taxa were selected by this stepwise procedure for generating the discriminant functions: Solanaceae, the Urticaceae/Moraceae group, the Chenopodiaceae/Amaranthaceae group, fern spores, *Myrica*, Euphorbiaceae, Myrtaceae, Ericaceae and Arecaceae.

Remarkably, these nine pollen taxa chosen through the stepwise process of discriminant analysis did not include the three main pollen taxa found on the Altiplano (Poaceae, Asteraceae and *Plantago*). Thus, the Altiplano vegetation (the centrepiece of this study) would be identified by the lack of the nine 'discriminator' taxa, rather than distinguished by the dominant taxa that are present on the landscape (which is problematic if these data are applied to fossil pollen studies). The omission of the three dominant taxa by the stepwise process is understandable from a statistical point of view, although it may not seem to make much ecological sense. All three taxa are somewhat 'cosmopolitan' to the central Andes and are present in all four vegetation groups; therefore they are not very good 'discriminator' variables in a statistical sense. In

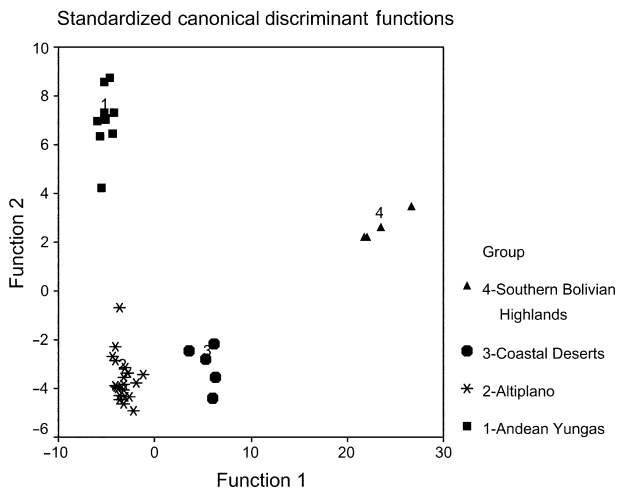


Figure 3 Surface sample groups plotted against discriminant functions 1 and 2.

Table 2 Scores (loadings) for the 12 taxa used in the discriminant function analysis

Pollen taxa	Function		
	1	2	3
Solanaceae	1.913	0.607	-0.050
Urticaceae/Moraceae	-0.089	1.815	0.169
Chenopodiaceae/Amaranthaceae	1.895	0.460	0.549
Fern spores	0.181	1.631	0.298
<i>Myrica</i>	1.014	-0.674	0.856
Euphorbiaceae	-1.048	0.021	0.473
Myrtaceae	-0.692	1.346	-0.085
Ericaceae	-0.176	3.104	0.268
Arecaceae	0.178	-2.389	-0.187
Poaceae	0.426	-0.081	0.275
Asteraceae	0.229	0.595	0.257
<i>Plantago</i>	0.275	0.459	-0.256

view of the ecological importance of these three taxa in the vegetative landscape of the Central Andes (and in our pollen data), we have chosen to include them in the derivation of the discriminant functions, bringing the number of taxa in the discriminant analysis to 12. Discriminant functions 1 and 2 explain 75.6% and 23.4% (respectively) of the total variance within the data set (cumulatively 99.0% of the total variance) (see Fig. 3 for sample scores, and Table 2 for taxon loadings).

After the discriminant analysis, 100% of the samples were correctly classified into their respective groups. However, discriminant analysis can go one step further and statistically test the strength of each of the groups. Using a self-validation technique, discriminant analysis removes each sample individually and tests the likelihood that it will be reclassified into its original group. The program then uses the discriminant functions to predict the likelihood (or 'probability of group membership', *sensu* Liu & Lam, 1985) that each sample will reclassify into its original group. Upon completion of this self-validation, 97.5% of the samples were still correctly classified.

Within each group, most pollen spectra were fairly similar to other members of the same group, as reflected by a moderately high average value (0.44) of 'probabilities of modern analogue' (*sensu* Liu & Lam, 1985) – a measure of the degree of internal variability within each group. Sample 11, which is located on the ecotone between groups 1 and 2, was the only sample not correctly classified upon self-validation (it was reclassified as group 2 instead of its original group, group 1). These results suggest that the classification of the samples into the four groups is statistically strong, and accurately represents the pollen data.

Pollen results

Overall, the pollen found in each of the four groups was indicative of the vegetation in each region (Fig. 4). The Yungas group (group 1) was dominated by Polypodiaceae fern spores (5–67%) and Urticaceae/Moraceae pollen (8–42%). Polypodiaceae is a very common family in the tropical lowlands, especially in the form of epiphytes (Mabberley, 1987). Urticaceae/Moraceae is also a very characteristic pollen type in tropical lowland forests and moist Andean forests. *Alnus* occurs at 4–13% in samples collected above 2300 m, reflecting the abundance of *Alnus* trees in the moist Andean forest belt between 2300 and 2800 m (Weng *et al.*, 2004). Although grass (Poaceae) is abundant in some samples, its frequency varies widely (5–57%) within this group. The occurrence of grass can be explained by our sampling locations, which were often in the vicinity of roads or other areas of human disturbance. Where natural or human-induced gaps occur in the tropical vegetation, grass is usually one of the first colonizers and proliferates in just a short time. Grass is also a prolific pollen producer and is known to be over-represented in pollen assemblages, especially in tropical areas where most of the plant species are not wind-pollinated (Colinvaux *et al.*, 1988; Bush, 2002). Other disturbance indicators can be seen in the small amounts of Asteraceae (1–20%), the Chenopodiaceae/Amaranthaceae families (0–11%) and *Plantago* (0–4%). The minor components in this Yungas group include trace amounts of pollen from a host of typical lowland families such as Melastomataceae, Apocynaceae, Piperaceae, Bignoniaceae, Malpighiaceae, Arecaceae, Myrtaceae and *Begonia*. Most of the plants in these families are animal-pollinated and therefore produce much less pollen than other wind-pollinated species. Thus, they are under-represented in the pollen assemblages.

The Altiplano group (group 2), not surprisingly, is dominated by the grasses, which make up 15–81% of the pollen assemblage. The other major taxa found in this group are all typical components of the region and can be found in abundance. They are Asteraceae (3–79%), *Plantago* (1–18%), fern spores (0–7%), Urticaceae/Moraceae (0–18%), Caryophyllaceae (0–8%) and *Cupressus* (0–7%). The *Cupressus* pollen is most likely from *Cupressus macrocarpa*, an exotic species that has effectively spread throughout the Altiplano (Cassinelli, 2000). Because of low pollen production, this

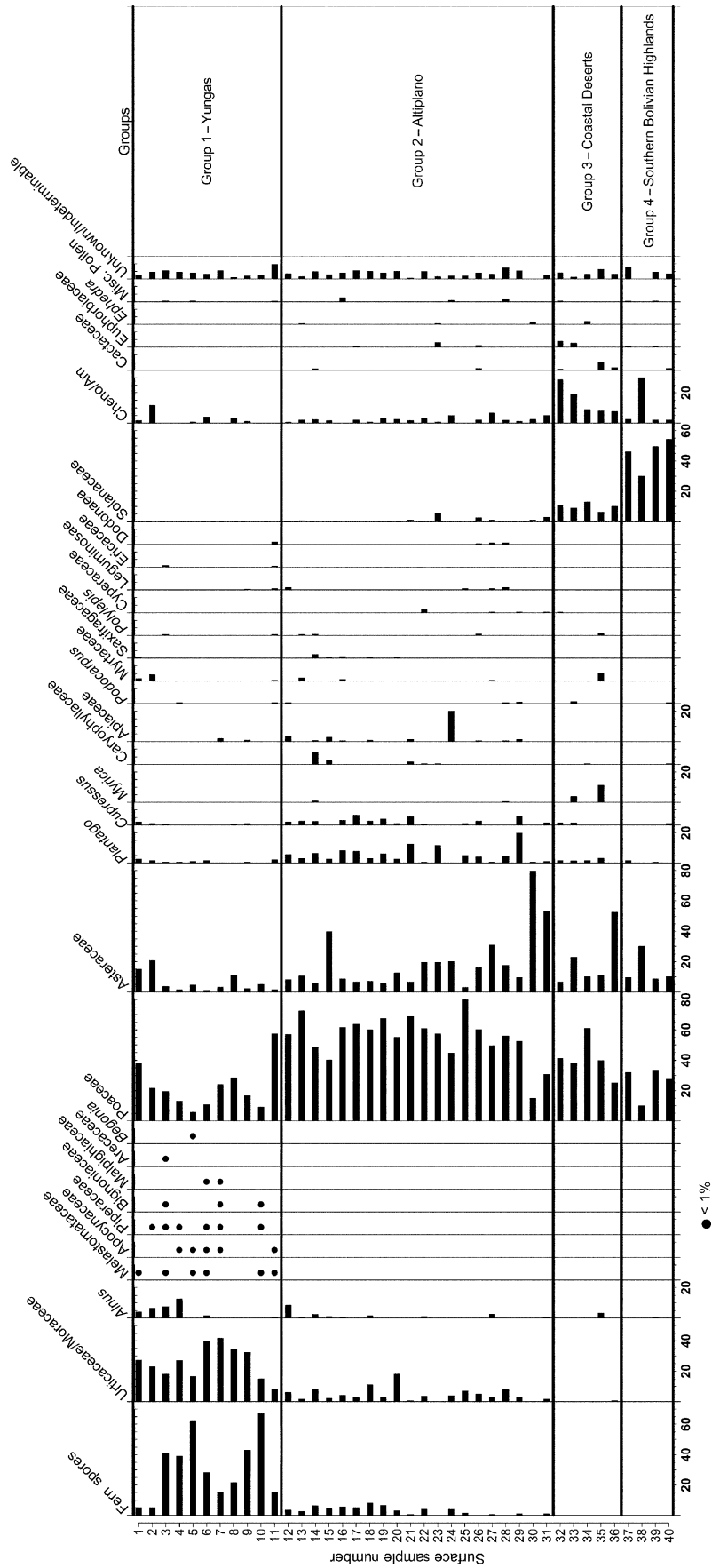


Figure 4 Pollen percentage diagram of the 40 surface soil samples.

genus is usually under-represented in the pollen assemblage (Reese & Liu, 2002), and is much more common in the landscape than the pollen suggests. The minor pollen taxa include *Alnus*, *Myrica*, Fabaceae, Myrtaceae, Saxifragaceae, *Polylepis*, Cyperaceae and Apiaceae. The Apiaceae pollen is probably derived from *Azorella yarita* (yareta), which is locally dominant in the 'bofedales'. Like *Cupressus*, yareta is typically under-represented in the pollen rain despite its local abundance.

Group 3, the Coastal Deserts, has a pollen assemblage that reflects the increasing dominance of the xerophytic shrubs and herbs. For example, percentages of grass (25–60%) and Asteraceae (6–52%) remain relatively high, while the Chenopodiaceae/Amaranthaceae group (7–30%) and Solanaceae (5–12%) increase significantly. In this group we also see increases in pollen from desert plant families like Cactaceae (0–5%), Euphorbiaceae (0–4%) and *Ephedra* (0–2%). Plants like ferns, the Urticaceae/Moraceae group and *Alnus*, whose pollen was so prevalent on the eastern, wetter slopes of the Andes, are notably absent in the western coastal regions.

The scrub desert of the Southern Bolivian Highlands (group 4) is a very distinctive group. Percentages of grass (10–33%) and Asteraceae (9–29%) are somewhat diminished, while the Solanaceae family (30–56%) becomes dominant. Minor taxa include Chenopodiaceae/Amaranthaceae (2–30%), while Cactaceae, Euphorbiaceae and *Plantago* are all under 5% of the total pollen sum. The pollen taxa typical of the puna ecosystems (e.g. *Cupressus*, *Polylepis* and Apiaceae) are all but absent in this group.

CONCLUSIONS

Distinct palynological signatures characterize the major vegetation zones of the central Andes region of South America. According to discriminant analysis, the surface samples can be divided into four discrete groups: (1) the Yungas, located on the eastern slopes of the Andes, (2) the Altiplano, (3) the Coastal Deserts of western Peru and Chile and (4) the scrub desert of the Southern Bolivian Highlands. The results from this study imply that the modern pollen rain in each region is representative of the regional vegetation.

In summary, the Yungas group is characterized by high percentages of Urticaceae/Moraceae pollen and fern spores along with trace amounts of pollen from common zoophilous taxa such as Piperaceae, Bignoniaceae and Malpighiaceae. The Altiplano group is characterized by the dominance of Poaceae pollen and other perennial herbs (*Plantago*) in combination with relatively high frequencies of Asteraceae pollen, which tend to increase slightly towards the southern (drier) locations of the Altiplano. The pollen data also hint at the strong precipitation gradient in the region. As precipitation decreases towards the south and west, the grasses and herbs give way to the more xerophytic, woody taxa like the Asteraceae and Solanaceae families (*Fabiana denudate* and *Fabiana ramulosa*) (Arroyo *et al.*, 1988; Latorre *et al.*, 2002). This trend continues

into the Coastal Desert vegetation zone to the west of the Andes. Here, the prominence of woody, xerophytic shrubs is coupled with the greater prevalence of true desert taxa like Chenopodiaceae/Amaranthaceae, Cactaceae and Euphorbiaceae. Aridity again defines the samples taken from the Southern Bolivian Highlands and the pollen assemblage reflects the dominance of Solanaceae and the Asteraceae plants in the area.

These modern pollen rain data were derived from the first systematic network of surface samples taken from a large geographical region across the entire central Andes, and encompass a variety of vegetation types from the Altiplano puna and the yungas to the coastal deserts and the Southern Bolivian Highlands. This database will serve to further the effectiveness of future fossil pollen studies in the region, by broadening our understanding of the modern relationships between pollen and vegetation in the central Andes, thus laying the groundwork for the derivation of pollen-climate transfer functions and response surfaces (Bush, 2000). Modern pollen rain data from different vegetation zones in alpine areas are especially vital for the development of the emerging field of ice-core palynology in tropical and subtropical regions (Thompson *et al.*, 1988, 1995; Liu *et al.*, 1998; Yao, 2000; Reese, 2003), because these data provide important clues to the provenance of pollen found in these ice cores. Data from this study have already been successfully applied to the palaeoecological interpretation of a 25,000-year fossil pollen record from the Mt Sajama ice cap of south-western Bolivia (Reese, 2003; K.-b. Liu, C.A. Reese & L.G. Thompson unpubl. data), and in a palynological study of annual snow accumulation in the Quelccaya ice cap of southern Peru (C.A. Reese & K.-b. Liu, unpubl. data).

ACKNOWLEDGEMENTS

The authors would like to thank Dr Keith R. Mountain and Jason K. Blackburn for their invaluable help in the field. We would also like to thank Mary Lee Eggart for cartographic assistance. This research was jointly supported by the Geography and Regional Science Programme, the Palaeoclimate Programme, and the Americas Programme of the National Science Foundation (NSF grants BCS-9906002, BCS-0117338 and BCS-0217321). Additional support for this project came from doctoral dissertation grants from the Geological Society of America, the Association of American Geographers, the Sigma-Xi National Research Society, and the Department of Geography and Anthropology at Louisiana State University.

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Editor: Philip Stott